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Habitat and Food Preferences in Six Eastern Pacific Chiton Species (Mollusca: Polyplacophora)

by

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Abstract. Habitat and diet were analyzed for six sympatric chiton species (*Mopalia hindsii, M. muscosa, M. ciliata, Katharina tunicata, Tonicella lineata,* and *Lepidochitona dentiens*) on a rock outcrop on Deception Island, Washington, U.S.A., using quadrat sampling and gut contents. Species showed significant differences in tidal height distribution, substratum slope, exposure, associations, and gut contents, although considerable overlap of food types occurred. *Katharina tunicata,* composing 72% of the chiton population in the study area, was a generalist, having a wide tidal height distribution and occurring on substratum slopes from 0 to 90 degrees. Its diet consisted of a variety of algal types including diatoms, *Ulva,* filamentous algae, and macrophytes. *Tonicella lineata,* composing 17% of the chiton population, was more specialized in microhabitat, having the highest percent cover of *Lithothamnion* and preferring slopes greater than 45 degrees and tidal heights below MLLW. *Lepidochitona dentiens,* the smallest and most specialized of the species, occurred only above MLLW and had a diet of almost exclusively diatoms (94%). *Mopalia ciliata* and *M. hindsii* had the highest percentages (25% and 18%) of invertebrates in their gut contents, while *M. muscosa* (4%) was more herbivorous. Differences in diet and microhabitat among these chiton species suggest that mechanisms such as resource partitioning or "indirect commensalism" may help maintain chiton diversity.

INTRODUCTION

CHITONS (Mollusca: Polyplacophora) are common members of intertidal communities. Many studies of the distribution, movement, interactions, and food preferences in chitons have concentrated on single species (BARNES, 1972; CAPLAN, 1970; DEMOPOLUS, 1975; DETHIER & DUGGINS, 1984; LYMAN, 1975; MOOK, 1983; NISHI, 1975; SMITH, 1975; WESTERSUND, 1975). Others have considered two or more species, but usually in relation to a limited number of ecological parameters (ANDRUS & LEGARD, 1975; CHELAZZI *et al.*, 1983; CONNOR, 1975; FITZGERALD, 1975; GLYNN, 1970; LANGER, 1978; MURDOCH & SHUMWAY, 1980). Studies comparing microhabitat and diet, two closely related ecological parameters, in a large number of sympatric species are almost lacking with the exception of those done by BARNAWELL (1954, 1960) and more recently by KANGAS & SHEPHERD (1984). Because many chiton species frequently inhabit the same locality, more such studies are needed to examine species differences and determine ecological mechanisms that would support such diversity.

The purpose of this study was to test for differences in habitat and food in six sympatric species of chitons. The species examined were *Mopalia hindsii* (Reeve, 1847), *M. ciliata* (Sowerby, 1846), *M. muscosa* (Gould, 1846), *Katharina tunicata* (Wood, 1815), *Lepidochitona dentiens* (Gould, 1846), and *Tonicella lineata* (Wood, 1815).

MATERIALS AND METHODS

General

This study was conducted during the summer of 1983 at Walla Walla College Marine Station near Anacortes, Washington, U.S.A. The primary study site was on the south side of Deception Island near Deception Pass, located off Whidbey Island at the eastern end of the Strait of Juan de Fuca. A rock outcrop (approximately 8 × 4.5 m) perpendicular to the shoreline and jutting out into the water was selected at this site. All six chiton species were found on the outcrop.

Transect lines were placed 0.5 m apart across the rock surface. Numbered tags were fastened to these lines at 0.5-m intervals providing a grid system that was used in sampling. Two sizes of quadrats were used in sampling: a 0.5 × 0.5-m quadrat and a 0.25 × 0.25-m quadrat. The smaller or "sampling quadrat" was a quarter section of the main, larger quadrat.

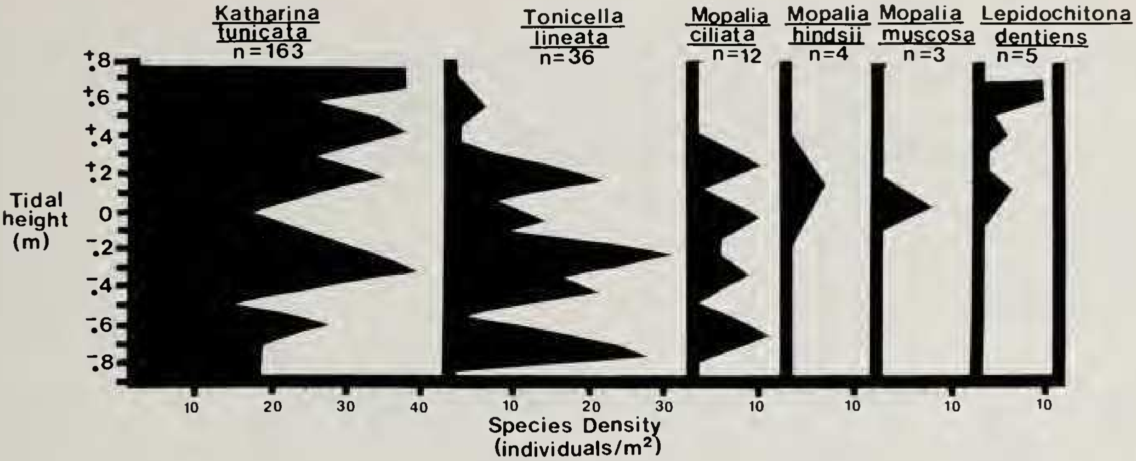

Figure 1

Density of six species of chitons at different tidal heights. Species density was computed from the total area sampled at 0.1-m intervals and the number of individuals of each species occurring in that interval.

Habitat

Habitat parameters evaluated and compared among the chiton species included tidal height, substratum type and slope, position and exposure to light on the rock surface, and percent cover of algae and invertebrates. The rock outcrop was sampled by placing the larger quadrats consecutively along transect lines over the rock surface. For each large quadrat, percent covers of algal species and invertebrates were estimated. One of the four quarter sections (*i.e.*, sampling quadrat) was randomly selected. All chitons in the sampling quadrat were identified following Kozloff (1974) and measured to the nearest millimeter. Tidal height was also determined for each sampling quadrat.

For each chiton within the sampling quadrat, the microhabitat was further characterized. Substratum slope was measured using a Brunton compass. Substratum type (rock, gravel-cobble, algae), degree of exposure (being in a pit, crack-crevice, groove, under algae, or fully exposed), position on the rock surface (top, side, bottom), and the presence of large barnacles (primarily *Balanus cariosus* [Pallas, 1788]) were recorded.

Because early sampling revealed that the greatest diversity of chiton species occurred on the sloping sides of the rock outcrop, the total sloping perimeter of the rock was sampled. The top horizontal surface of the rock was less completely sampled with quadrats placed only between alternate transect lines.

Food

Gut contents were examined to determine food preferences of the chiton species. Specimens were collected near the rock outcrop during both low and high tides. SCUBA was used during high tides. After collection, animals were initially preserved in a 10% formalin solution, and later transferred to 70% alcohol. The stomach and intestine of each animal were dissected out and the contents removed. In those species in which material was abundant, samples were spread over three microscope slides. However, in *Tonicella lineata* and *Lepidochitona dentiens,* gut contents were often sufficient for only 1 or 2 slides. This was partly due to the small size of the animals.

Material in the gut contents was identified, measured, and compared among the chiton species. The gut contents on each slide were scanned three times from left to right. Each time a food item was seen, an estimate of its projected surface area was obtained by counting the number of 0.5-mm squares it covered on a 1 × 1-cm ocular grid. From this area value, the percent of that food in the diet was calculated for each individual and species.

Specific identification of gut contents was not always possible. Most algal material was identified to genus. Invertebrates were identified to general taxonomic group, such as amphipod, barnacle, hydroid, or polychaete.

Individual food items were placed in food categories for species comparison. Food categories, similar to those of Steneck & Watling (1982), were established. These included diatoms, filamentous algae (*e.g., Polysiphonia, Pterosiphonia, Antithamnion,* and *Cladophora*), *Ulva,* soft encrusting red algae (*e.g., Hildenbrandia* and *Petrocelis*), hard encrusting algae (*Lithothamnion*), macrophytes consisting of algae with several cell layers and forming large erect thalli usually branching or blade-like (*e.g., Gigartina, Hedophyllum,* and *Fucus*), and invertebrates (*e.g.,* bryozoans, hydroids, barnacles, bivalves, gastropods, polychaetes, and various larvae). The algal groupings were at least partially designed to reflect size, structure, toughness, and resistance to being scraped off the rock surface.

Table 1

Summary of species comparisons based on statistical tests and subjective interpretations of observations.

	Mopalia hindsii	*Mopalia ciliata*	*Mopalia muscosa*	*Katharina tunicata*	*Tonicella lineata*	*Lepidochitona dentiens*
Habitat study						
Percent of total sampled	*n* = 4 (2%)	*n* = 12 (6%)	*n* = 4 (2%)	*n* = 163 (72%)	*n* = 36 (16%)	*n* = 5 (2%)
Average length (cm)	6.3	4.4	5.6	5.9	2.7	1.1
Tidal range (m)	0–+0.4	−0.8–+0.4	0–+0.3	−0.9–+0.8	−0.9–+0.7	0–+0.8
Distribution†	narrow	broad (−)	narrow	broad (+)	broad (−)	narrow
Substratum slope >45°	X	X			X	
<45°						X
0–90°			X	X		
Position or exposure						
Sides	X	X	X	X	X	
Top				X		X
Under overhang	X	X			X	
Among barnacles	X	X		X		X
Associations						
Diatoms	X	X	X	X	X	X
Soft encrusting	X	X	X		X	X
Lithothamnion					X	
Ulva				X		X
Filamentous			X			
Macrophytes						
Invertebrates	X	X	X			X
Diet study*						
Diatoms	X	X	X	X	X	X
Soft encrusting						
Lithothamnion					X	
Ulva			X	X		
Filamentous	X	X				
Macrophytes				X		
Invertebrates	X	X				

* Diet was determined from gut contents removed from different individuals not included in the habitat study. In the diet study, the sample size was eight for all species except *Lepidochitona dentiens* in which it was six.

† For each distribution listed as broad, the center of abundance is indicated as − or + for centers below or above MLLW, respectively.

RESULTS

Habitat

Katharina tunicata was clearly the dominant species at the study site, composing about 72% of the chiton population (Table 1). *Tonicella lineata* was the next most common species composing 17% of the population, while the remaining four species were considerably less abundant.

Chiton species showed significant (Chi-square tests, $P < 0.005$) differences in tidal height distribution at 0.1-m intervals through the sampling range (Figure 1). Although both had wide distributions, *Katharina tunicata* was more abundant above 0 m tidal height or mean lower low water (MLLW), whereas *Tonicella lineata* was more abundant below MLLW. *Lepidochitona dentiens* appeared limited in its distribution to above MLLW.

Chiton species differed further relative to substratum angle (Table 1). To determine species differences, substratum angle was divided into 15-degree intervals from 0 to 90 degrees. The number of individuals of each species occurring at each slope interval was computed. A significant (Chi-square test, $P < 0.005$) difference existed in species distribution relative to substrate slope. *Tonicella lineata, Mopalia hindsii,* and *M. ciliata* seemed to prefer slopes of greater than 45 degrees. In contrast, *Lepidochitona dentiens* occurred on more horizontal substrata. *Katharina tunicata* appeared to have an almost normal distribution centered around 45 degrees.

Position or exposure on the rock outcrop differed among the chiton species (Table 1). Preference for position and exposure on the rock surface was tested using Chi-square tests. Six tests were performed independently on the number of individuals of each species associated with each of the following categories: being under a rock or rock overhang, on the sides of a rock, on the top of a rock, under algae, in a groove-crack-crevice, or among large barnacles. Significant ($P < 0.05$) species differences were found in three of the six categories: presence on the top of the rock,

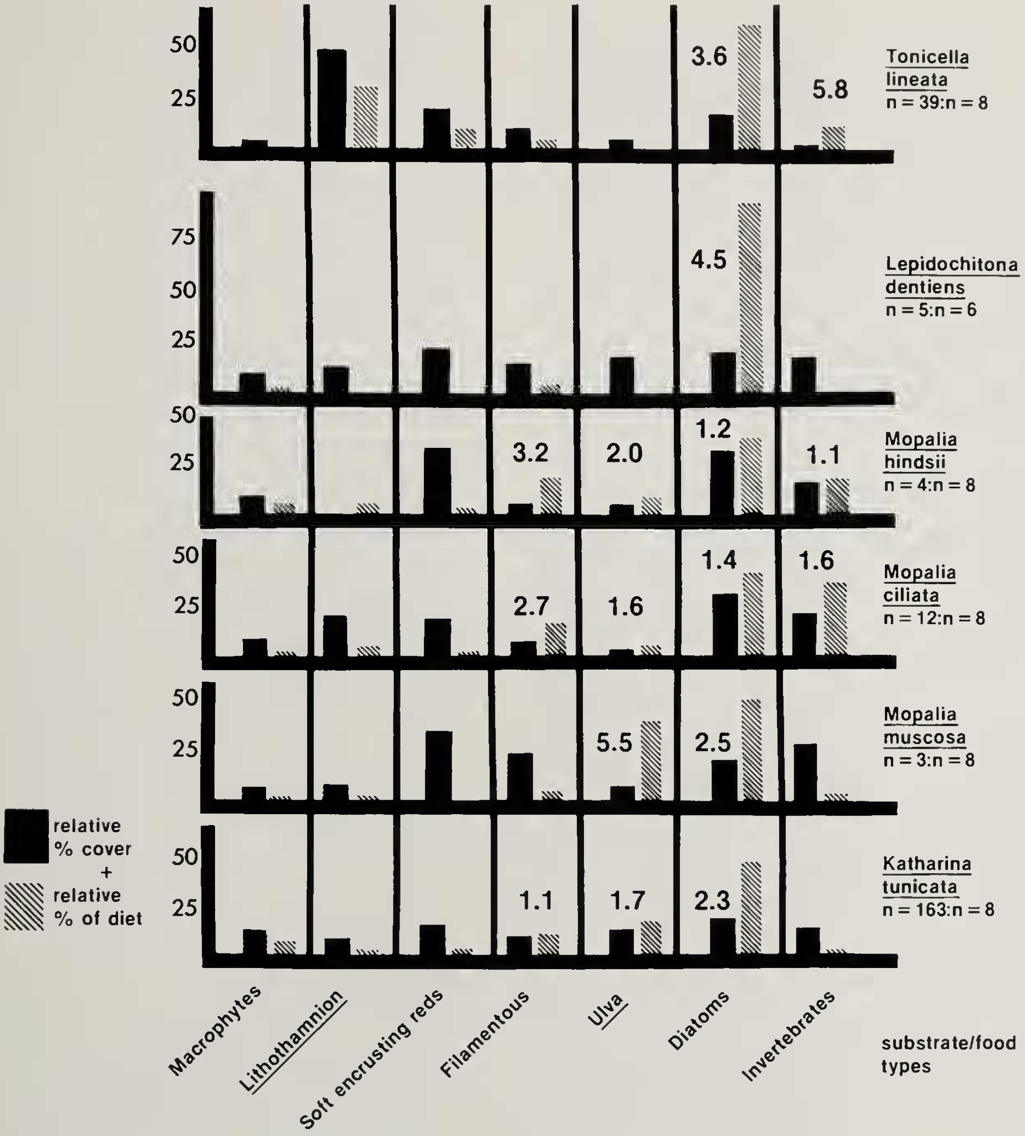

Figure 2

Comparison of percent of diet (crosshatched bars) with percent cover (solid bars) for the seven food groups and six chiton species. Values in some boxes are ratios >1, which suggest "selective feeding." The first *n* value given is for percent cover, the second for diet.

under a rock or rock overhang, and among large barnacles. *Lepidochitona dentiens* was limited exclusively to the top horizontal surface of the rock outcrop. In contrast, *Tonicella lineata, Mopalia ciliata,* and *M. hindsii* were found primarily on the sloping sides and under rock overhangs. *Katharina tunicata* was found more uniformly both on the sloping sides and top horizontal surface.

Owing to the topography of the rock outcrop, the tidal height, substratum slope, and position or exposure on the rock surface may be confounding variables at the study site. Results suggesting significant species differences in all three parameters may therefore be due to but a single factor or some combination of the three.

Microhabitat differences also existed among the chiton species in associations with algae and invertebrates (Table 1; Figure 2, solid bars). Species differed with respect to *Ulva*, to *Lithothamnion*, and to invertebrates (one-way ANOVA, $P < 0.001$) and to soft encrusting red algae (one-way ANOVA, $P < 0.05$). Particularly note the high association of *Tonicella lineata* with *Lithothamnion.*

Food

The guts of chiton species differed (one-way ANOVA, $P < 0.05$) in their contents of *Ulva* and diatoms (Table 1; Fig. 2—crosshatched bars) and possibly ($P < 0.09$) in their contents of *Lithothamnion,* filamentous algae, and invertebrates. Invertebrates, primarily worms and amphipods, were frequently associated with filamentous red algae in the gut contents of *Mopalia hindsii* and *M. ciliata.* Perhaps living among the filaments, such worms and amphipods are ingested with the algae. Whole barnacles and barnacle plates were common in the gut contents of *Mopalia* spp. Separation of invertebrates into several separate food categories would be helpful in distinguishing chiton feeding differences within this broad category.

Figure 2 permits a comparison for each chiton species of percent of food type in the diet to percent cover in the microhabitat. Ratios greater than one suggest positive selectivity in feeding as opposed to random browsing. All species of chitons had a larger proportion of diatoms in their diets than in the microhabitats. This is particularly noticeable for *Tonicella lineata* and *Lepidochitona dentiens,* the two smallest species. In addition to positive selection, such high ratios could result from easier identification and(or) greater preservation in the gut as compared with other foods.

In *Mopalia ciliata* and *M. hindsii* the high gut content to microhabitat ratios of filamentous algae also suggest selective feeding. Similarly, *M. muscosa* appeared to select *Ulva.* The particularly high ratio of invertebrates in *Tonicella lineata* was primarily due to a single chiton with a large crustacean in its gut. Hence, this value may not reflect a real food preference for invertebrates. Direct comparisons of food types in the microhabitat with gut contents for individual chitons, a closer examination of less conspicuous food items in the microhabitat (smaller algal and invertebrate species), large sample sizes, and performing food preference experiments are needed to further confirm dietary differences and the presence of selective feeding.

DISCUSSION

Differences in microhabitat (*i.e.,* tidal height, position and exposure on the rock surface, substratum slope, and chiton-algal or chiton-invertebrate associations) may ecologically separate the chiton species studied. Because a limited area and tidal range were sampled, the observed relation of chiton species with intertidal height may not hold for other localities. LANGER (1978) found a spatial separation of three species of chitons in relation to depth. My study and investigations by ANDRUS & LEGARD (1975) and BARNAWELL (1954) suggest that other differences besides tidal height (*i.e.,* exposure or associations) may also be important in spatially segregating chiton species.

ANDRUS & LEGARD (1975) found *Tonicella lineata* to occur only in the presence of encrusting coralline algae. This same association appears in my study. *Tonicella lineata* always occurred on or near the encrusting calcareous alga *Lithothamnion,* for which it had the highest percent cover (48%). This factor alone clearly separated it spatially from the other species.

Significant differences in specific food items or food groups found in gut contents indicate that diet varies among these species. The high percent of *Lithothamnion* in the gut contents of *Tonicella lineata* agrees with similar findings of DEMOPOLUS (1975), BARNES (1972), and BARNES & GONOR (1973). The higher percent contribution of animal versus plant material in the gut contents of *Mopalia ciliata* (25%), and *M. hindsii* (18%) than in *M. muscosa* (4%) is in striking agreement with observations by BARNAWELL (1954, 1960). This difference appears especially important in ecologically separating *M. hindsii* and *M. ciliata* from *M. muscosa,* which were quite similar in other niche dimensions.

GAINES (1985) has found that *Katharina tunicata* readily feeds on the relatively large, foliaceous red alga *Iridaea.* DAYTON (1975) has observed that *K. tunicata* browses extensively on large *Hedophyllum.* My findings that *K. tunicata* had the highest percentage (although still small) of macrophytes in its diet agree with this association.

Diet appears to be an important ecological parameter separating sympatric chiton species. Diet differed among 16 species of chitons examined on a boulder slope in south Australia (KANGAS & SHEPHERD, 1984). Six were herbivores, seven omnivores, and three carnivores. Within these feeding types some were generalists, others specialists. A similar range of feeding strategies was found in the six species I studied. The smallest chiton, *Lepidochitona dentiens,* appeared quite specialized in diet, relying almost exclusively (94%) on diatoms. The next smallest species, *Tonicella lineata,* had a greater variety of both plant and animal food types in its gut contents, although it did have the highest percentage (16%) of *Lithothamnion,* clearly distinguishing it from all other species. The remaining species tended to be omnivorous, having a wide variety of both plant and animal material in their guts. However, *Katharina tunicata* and *Mopalia muscosa,* with 99% and 96% plant material in their diets respectively, were clearly more herbivorous than *M. hindsii* (82%) and *M. ciliata* (75%). These latter two species had the highest percentages of animal material (primarily barnacles and amphipods) of all six chiton species. Differences in diet as well as microhabitat could result from resource partitioning.

With niche overlap in both microhabitat and food among the chiton species in this study, competition might result. Indirect evidence for space competition was suggested by the drop in density of *Katharina tunicata* near MLLW where three other species had high densities (Figure 1). To test for competition, however, experiments involving both addition and removal of individual chiton species would be necessary.

An alternative relationship to competition might exist among certain of these chiton species as suggested by the work of DETHIER & DUGGINS (1984) who demonstrated an "indirect commensalism" between *Katharina tunicata* and two limpet species. Although these species are potential competitors due to partial food type overlap, Dethier and Duggins showed that the presence of *K. tunicata* actually benefited the limpets. *Katharina tunicata* fed on competitively dominant macroalgae (as well as diatoms), thus enhancing the growth of diatoms, which are the primary food of limpets.

That *Katharina tunicata* may have a similar role with certain chiton species is suggested by comparing the Deception Island observations with preliminary observations at a second ("Dock") site near the Anacortes State Ferry Dock. Diatoms had a high percent cover and were a major prey species at the Deception Island site (Figure 2), whereas macroalgae (such as those consumed by *K. tunicata*) were relatively less abundant. The large population of *K. tunicata* may be removing dominant macroalgae species, thus facilitating diatom growth. In contrast, at the "Dock" site, macroalgae (including *Ulva* sp.) had a high percent cover while diatom growth was greatly reduced. At this site, the population density of *K. tunicata* was considerably lower than at Deception Island ($4/m^2$ vs. $22/m^2$). Two species, *Tonicella lineata* and *Lepidochitona dentiens,* that appeared to rely heavily on diatoms for food (Figure 2), also had lower densities ($3/m^2$ vs. $6/m^2$ and $0/m^2$ vs. $1/m^2$ respectively) at the "Dock" site than at Deception Island while the density of the remaining chitons (*Mopalia* spp.) remained the same. Thus, extensive grazing by *K. tunicata* on macroalgae might enhance diatom and other microalgal growth for use by other chiton species, and indirectly help to sustain or increase chiton diversity.

The interactions and relationships among the chiton species in my study that maintain diversity are certainly not clear. Further manipulative experiments are needed to better define them.

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